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Morphological Variation and Environmental Conditions of *Syzygium* (Myrtaceae) in the Bonin Islands

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To understand the morphological and ecological diversity of *Syzygium* in the Bonin Islands, we examined 269 individuals from 37 localities in the Bonin Islands and the Nansei Islands for vegetative and floral characters. The vegetation of their respective habitats was also examined as an indicator of environmental conditions. Three groups of *Syzygium* in the Bonin Islands were distinguishable from the Nansei Islands group by principle component analysis (PCA). These four groups had unique morphological sets. The three groups in the Bonin Islands generally grow in different vegetation and seldom occur sympatrically, suggesting habitudinal segregation among the groups. One group of plants on the Bonin Islands is distributed on both the Chichi-jima Islands and the Haha-jima Islands and shows remarkable morphological variation of the Haha-jima Islands compared with those of the Chichi-jima Islands. In particular, many individuals in the southern area of the Haha-jima Islands have peculiar morphological features not found in the others. Furthermore, these distinctive Haha-jima individuals grow in *Distlylium* - *Schima* dry forests, which are rare for this group on the Chichi-jima Islands. The morphological differentiation of this group may represent an initial stage of the evolutionary process of adapting to environmental conditions.

Key words: Bonin (Ogasawara) Islands, morphological variation, Myrtaceae, oceanic island, plant community, principal component analysis, Ryukyu Islands, *Syzygium buxifolium*, *Syzygium cleyerifolium*

Endemic congeners derived from a common ancestor and growing on nearby, isolated islands, exhibit peculiar morphological characters depending on their different habitats (Carlquist 1970, Bramwell 1972, Kawakubo 1986, Shimizu & Tabata 1991, Baldwin 1997, Stuessy *et al.* 1998). This means that adaptive radiation is one of the most important processes of speciation in the islands (Carlquist 1970, Bramwell 1972, Stuessy *et al.* 1998). On the other hand, one species in the islands often occurs in various habitats as compared with its counterparts on the continent (Carlquist 1970, Hamann 1979, Mueller-Dombois 1994), showing morphological variation related to each habitat (Carlquist 1970, Hamann 1979). These occurrences are important for understanding how each morphological feature and ecological circumstance has been involved in the process of adaptive radiation. Similar phenomena are found in *Syzygium* in the Bonin Islands (Shimizu 1984), oceanic islands located about 1000km south from the Japanese mainland.

The plants of *Syzygium* in the Bonin Islands have currently been treated taxonomically as *Syzygium buxifolium* Hook. et Arn. var. *cleyerifolium* (Yatabe) Tateishi (Tateishi 1999). This taxon, however, shows considerable morphological and ecological diversity, and it has been subjected to different taxonomic treatments by different authors, all of whom have included in their studies *Syzygium* plants on the Nansei Islands (Hatusima 1976, 1989, Toyoda 1981, Yamazaki 2001). In order to understand the diversity of *Syzygium* plants in the Bonin Islands, it is nec-

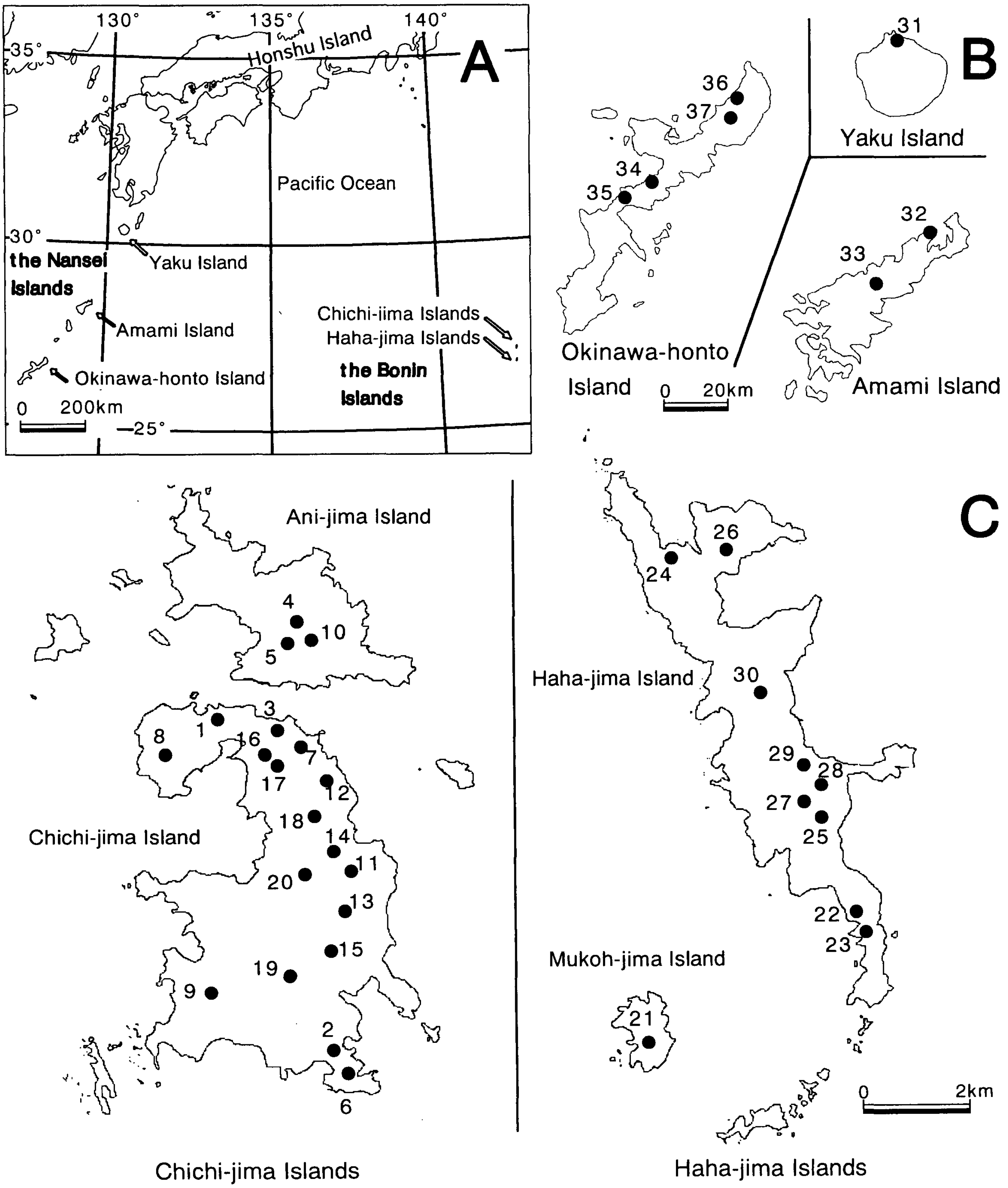

FIG. 1. Locations of study sites. A: locations of the Bonin Islands and the Nansei Islands, B: 7 collection sites on Yaku Island, Amami Island, and Okinawa-honto Island (the Nansei Islands), C: 30 collection sites in the Chichi-jima Islands and the Haha-jima Islands (the Bonin Islands).

essary to analyze relationships between morphological variation and environmental conditions.

The purpose of this paper is to reveal the morphological variation of *Syzygium* in the Bonin Islands, to compare these morphologies to that in the Nansei Islands, and to examine the environmental conditions related to the morphological variation of *Syzygium* in the Bonin Islands.

Material and Methods

Morphological measurements and analyses

We investigated 268 flowering individuals from 30 localities in the Bonin Islands and 6 localities in the Nansei Islands during 1999-2001. In addition, one individual transplanted from Yaku Island of the Nansei Islands into the Botanical Garden of the University of Tokyo was examined (Fig. 1, Table 1). We measured stem height and maximum width of tree crown, and then collected several flowers (fixed with FAA) and shoots at the canopy of each individual. Five morphological leaf characters (see Fig. 2) were measured by a digital slide caliper (Mitsutoyo Co., Ltd.) for three fresh leaves per individual at the second node from the top. The leaf blade thickness was measured by caliper at the center of the maximum transversal width of the leaf. Five floral characters (see Fig. 2) were measured on three flowers per individual using a digital microscope (VH-6300, Keyence Co., Ltd.) at 50 magnifications. Seeds and fruits were collected from 143 of 269 flowering individuals, and the diameters of five fresh samples per individual were measured by caliper (Fig. 2).

Statistical analyses were performed using the mean values for the characters of each individual. In order to reveal the degree of morphological variation, principal component analysis (PCA) was performed using a correlation matrix of all of the measured characters (see Table 2). The scores of each component were standardized (mean = 0, standard deviation = 1).

Voucher specimens of all the individuals examined were deposited in the Makino Herbarium, Tokyo Metropolitan University (MAK).

Environments and vegetation survey

In order to determine the environmental conditions of *Syzygium* habitat in the Bonin Islands, we conducted

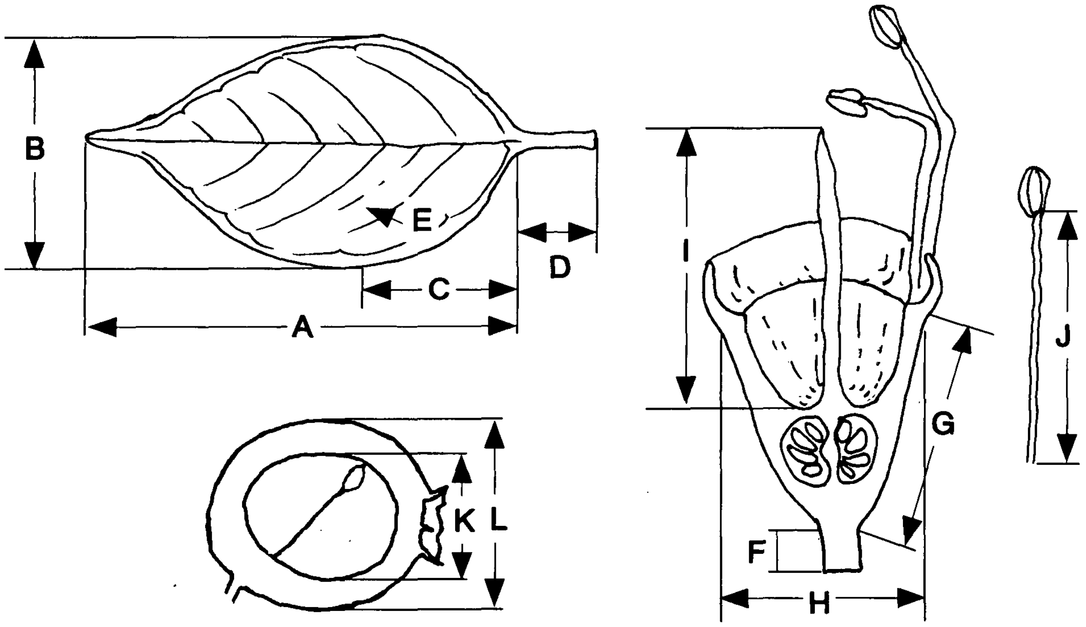

FIG. 2. Measured characters of leaf, flower, and fruit. A: leaf blade length, B: leaf blade width, C: length from base of leaf blade to maximum leaf blade width, D: petiole length, E: leaf blade thickness at the maximum leaf blade width, F: pedicel length, G: calyx tube length, H: calyx tube width, I: style length, J: filament length, K: seed diameter, L: fruit diameter.

TABLE. 1. Samples of *Syzygium* in the Bonin Islands and the Nansei Islands.

Study site code	Locality	Number of Samples	Altitude (m)	Number of samples for evaluation of pre-dawn water potential samples
The Bonin Islands				
The Chichi-jima Islands				
The Ani-jima Island (area: 7.85km^2, highest altitude: 254m)				
4	Takinoura, northern area	11	85-100	
5	Mt. Mikaeri-yama, northwest slope	14	105-130	
10	Mt. Mikaeri-yama, northern ridge	3	165-210	
The Chichi-jima Island (23.95km^2, 326m)				
1	Miyanohama, eastern area	10	10-45	6
2	Nishikaigan area, southwest area	1	75	
3	Mt. Denshin-yama, western ridge	15	70-100	7
6	Tatsumizaki	1	130	
7	Nagasaki	24	120-165	14
8	Mt. Mikazuki-yama, southwest ridge	1	150	1
9	Mt. Taka-yama, southeast area	8	150-210	
11	Higashidaira, Mt. Hatsune-yama, southwest ridge	17	200-220	
12	Asahidaira region	3	205-220	
13	Higashidaira, southern area	6	220-235	
14	Higashidaira, northern area	8	200-265	1
15	Shigure-yama region	12	220-270	7
16	Mt. Asahi-yama, near the summit	4	250-265	
17	South peak of Mt. Asahi-yama	4	250-270	
18	Mt. Yoake-yama, southeast slope	23	235-295	9
19	Mt. Tsutsuji-yama, northwest ridge	3	300	
20	Mt. Chuuou-zan, southern peaks	14	300-310	4
The Haha-jima Islands				
The Mukoh-jima Island (1.4km^2, 137m)				
21	Kopepehama, northeast area	6	50-110	
The Haha-jima Island (20.8km^2, 462m)				
22	Minamizaki, near the Omotohama	21	35-65	
23	Minamizaki, near the Yotsukaigan	10	60	
24	Ohsawakaigann, northern area	4	85	
25	Tamagawa dam, southern area	7	190	
26	Mt. Higashi-yama, southwest ridge	6	180-220	
27	Mt. Chibusa-yama, near the Mt. Kenzaki-yama	3	200	
28	Mt. Chibusa-yama, near the Mt. Funaki-yama	5	275-380	
29	Mt. Chibusa-yama, southeast ridge	7	330-380	
30	Mt. Sakai-gatake, near the summit	2	430	
The Nansei Islands				
The Satsunan Islands				
The Yaku Island (502.87km^2, 1935m)				
31	Shitogo	1	0-200?	
	(transplanted in Koishikawa Botanical Garden, Tokyo)		(20)	
The Amami Island (127.87km^2, 694m)				
32	Cape Imai	1	95	
33	Mt. Matsunaga-yama, northern slope	1	225	
The Ryukyu Islands				
The Okinawa-honto Island (1201.27km^2, 498m)				
34	Kenminnomori Forest in Onna village	4	90-110	
35	Mt. Ishikawa-dake, western ridge	1	135	
36	Forest park in Kunigami village	7	200-270	
37	Ohguni forest-road, southern area of Mt. Yonaha-dake	1	300	
Total		269		49

companion surveys as follows:

1) *A survey of floristic composition in plant communities where* Syzygium *plants grows.*
Floristic composition in plant communities is highly sensitive to environmental conditions (Braun-Blanquet 1964, Kent & Coker 1992); hence, it is a good indicator of their environmental conditions. The floristic composition in plant communities around all 253 individuals of *Syzygium* in the Bonin Islands was surveyed at the top layer of the plant communities according to the plant sociological method (Braun-Blanquet 1964). The plot size (0.5 - 150m^2) was decided according to the concept of minimal area (Mueller-Dombois & Ellenberg 1974) and community types. Because several *Syzygium* plants often occurred in one surveyed plot, the total number of plots came to 152 covering all 253 individuals. The taxonomic treatment of floristic elements in this vegetation survey followed Ono & Kobayashi (1985).

Vegetation data were classified by the TWINSPAN method (Hill 1979). Optional fields of analysis were defaulted except for pseudospecies cut levels (the cut levels established at five levels, coverage of each species 1, 2, 3, 4, and 5). *Syzygium* plants were treated as one element of the floristic composition in this analysis because the division of *Syzygium* into some groups seriously influenced the classification of plant communities.

2) *A survey of soil water contents on the Chichi-jima Island.*
The average annual rainfall on the Chichi-jima Island over the past three decades has been 1235mm; extreme soil-water deficits occur frequently, especially in July and August (Oka *et al.* 2001). Therefore, the soil water content is regarded as one of the most important environmental factors for plants in the islands. Soil water content in the habitat of *Syzygium* was analyzed from pre-dawn leaf water potential, because it reflects the soil water content adjacent to the root (Larcher 1999). We measured pre-dawn leaf water potential in August, which is the driest month of the year (measurements for the Chichi-jima Island for August, 1999 were: precipitation, 67.5mm; potential evapotranspiration, 157.6mm. Oka *et al.* 2001). One leaf per individual was collected at pre-dawn from 49 individuals on the Chichi-jima Island (Table 1); the leaves were immediately taken to the laboratory to be measured by a psychrometer (Tru Psi, DECAGON Co. Ltd.) to estimate leaf water potential. There had been no rainfall for two weeks prior to the survey on 21 and 22 August of 1999. The data for pre-dawn leaf water potential of each individual in the two days are represented by the mean values.

Results

Morphological variation of Syzygium *in the Bonin Islands and the Nansei Islands*
The first three principal components of the floral and vegetative characters in Table 2 explain 81.2 % of the total variation. The first component was the size factors of leaf and flower because these characters had mainly high factor loadings. The second component was tree size factor; the third component, pedicel length.

A three-dimensional diagram for the first three components of PCA (Fig. 3) show that the individuals in the Nansei Islands assembled as one group, and were clearly distinguished from the individuals of the Bonin Islands by the third component, pedicel length. Two assemblages could be recognized within the Chichi-jima Islands, and one within the Haha-jima Islands. Because one of the two assemblages in the Chichi-jima Islands almost overlapped with that of the Haha-jima Islands (Fig. 3), these were recognized as one group. As a result, we recognized three groups, A, B and X, in the Bonin Islands and the Nansei Islands, as shown in Fig. 3.

In order to understand the morphological variation within groups A and B, PCAs were performed using 120 individuals of group A, and 133 individuals of group B, respectively. The first three principal components in Table 3 explained 69.5 % of the total variation in group A. The first component was leaf size factor; the second, flower size factor. Tree size characters largely affected the third component. In the result of PCA for group A (Fig. 4), the individuals in the Haha-jima Islands had broader variation on the second component than those in the Chichi-jima Islands. The individuals in the Haha-jima Islands with high scores on the first two components hardly overlapped with those of the Chichi-jima Islands (Fig. 4).

The first three principal components in Table 4 explained 68.1 % of the total variation in group B. The first component was leaf size factor; the second, tree size factor. Flower size characters except for pedicel length largely affected the third component. A three-dimensional diagram of the first three principal components depicted two distinct groups, B1 and B2, within group B (Fig. 5). The second component established most of the difference between the two groups.

In the comparison of morphological characters among the groups (Fig. 6), the style length was an important character for distinguishing groups B1 and B2 from the others (Fig. 6m). This does not support the view of Yamazaki (2001), who distinguished *Syzygium* of the Bonin Islands from that of the Nansei Islands by the style length. *Syzygium* plants of the Bonin Islands differed from those of the Nansei Islands mainly by their differences in pedicel length, although their variations overlapped a little (Fig. 6j). Group B1 was significantly different from group B2 in the fruit and seed features (Fig. 6o, p) and in several vegetative ones (Fig. 6c, d, f - h, o, and p), especially tree height and architecture (Fig. 6a, b). On the other hand, floral characters (Fig. 6j, k, m, and n) did not differ between the two groups, except for pedicel length and calyx tube width (Fig. 6j, l).

Distribution and environmental conditions of each group of Syzygium *in the Bonin Islands*

Group A was found at various altitudes from 35m to 430m in the Haha-jima Islands, but was found mainly in the mountain area from 220m to 310m alt. in the

TABLE. 2. Results of principal component analysis for floral and vegetative characters in 269 individuals of *Syzygium* in the Bonin Islands and the Nansei Islands. Code corresponds to that in Fig. 2

		Component		
Code	Trait	1	2	3
	stem hight	-0.31	0.87	0.18
	maximum width of tree crown	-0.21	0.90	0.02
A	leaf blade length	-0.77	0.44	0.22
B	leaf blade width	-0.84	0.25	0.09
C	length from base of leaf blade to maximum leaf blade width	-0.65	0.51	0.09
D	petiole length	-0.73	0.43	0.27
E	leaf blade thickness	0.22	-0.42	-0.66
F	pedicel length	-0.03	-0.04	0.92
G	calyx tube length	-0.89	0.15	-0.02
H	calyx tube width	-0.90	0.16	-0.07
I	style length	-0.80	0.21	0.43
J	maximum length of filament	-0.87	0.19	0.22
Eigenvalue		5.46	2.59	1.70
Cumulative variance (%)		45.48	67.03	81.21

Chichi-jima Islands (Fig. 7). Groups B1 and B2 grow in close proximity in many sites investigated in the Chichi-jima Islands (the sites 3, 4, 5, 7, 10, 11, and 12 in Figs. 1 and 8).

The vegetation including *Syzygium* plants in the Bonin Islands was classified into 25 communities (Fig. 9) by TWINSPAN method. In this analysis, the plural taxa, which are difficult to discriminate clearly from each other, were treated as one floristic element; for example, *Pouteria obovata* - *P. obovata* var. *dubia*, *Neolitsea aurata* - *N. gilva*, *Osteomeles boninensis* - *O. lanata*, *Ilex mertensii* - *I. percoriacea*. The vegetation types of these communities were identified according to the criteria of Shimizu & Tabata (1991), considering the floristic composition, vegetation height, and layer structure in the plant communities. Group A mainly grows in *Pinus* - *Schima* mesic forest and *Rhaphiolepis* - *Livistonia* dry forest and partially in *Distlylium* - *Schima* dry forest; group B1 in *Distlylium* - *Schima* dry forest; and group B2 in *Distlylium* - *Pouteria* dry scrub. Thus, each group showed a tendency to grow in different plant communities. In particular, the plant communities where groups B1 and B2 occur were clearly different from each other (Fig. 9), although both groups were often found adjacently within the same study site (Fig. 8). Groups A and B1 occur sympatrically in only 3 (16 - 96m^2) of 152 surveyed plots (Fig. 9). Thus, habitudinal segregation was generally found among the three groups.

Seven (community nos. 1, 4, 5, 8, 9, 10, and 12) of eleven communities (community nos. 1 - 6, and 8 - 12) where group A grew were distributed in common between the two islands (Fig. 9). Of the com-

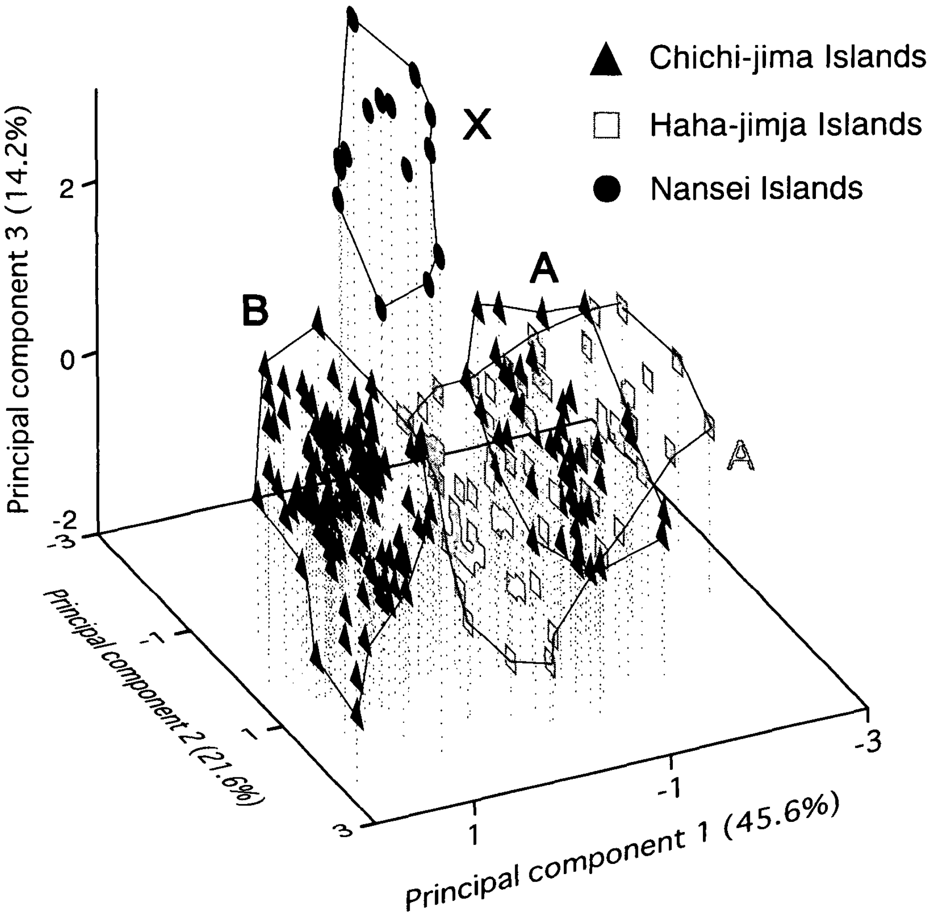

FIG. 3. Three-dimensional diagram of 269 individuals of *Syzygium* in the Bonin Islands (the Chichi-jima Islands and the Haha-jima Islands) and the Nansei Islands based on principal component analysis of floral and vegetative characters.

TABLE. 3. Results of principal component analysis for floral and vegetative characters in 120 individuals of Group A of *Syzygium* in the Chichi-jima Islands and the Haha-jima Islands. Code corresponds to that in Fig. 2.

Code	Trait	Component 1	Component 2	Component 3
	stem hight	-0.20	-0.09	0.91
	maximum width of tree crown	-0.06	0.08	0.93
A	leaf blade length	-0.92	-0.27	0.12
B	leaf blade width	-0.87	-0.27	0.02
C	length from base of leaf blade to maximum leaf blade width	-0.91	-0.09	0.21
D	petiole length	-0.67	-0.27	0.01
E	leaf blade thickness	0.48	0.40	-0.15
F	pedicel length	-0.11	-0.30	-0.01
G	calyx tube length	-0.10	-0.82	-0.08
H	calyx tube width	-0.23	-0.80	0.03
I	style length	-0.29	-0.82	0.13
J	maximum length of filament	-0.21	-0.84	-0.01
Eigenvalue		3.35	3.18	1.80
Cumulative variance (%)		27.95	54.47	69.45

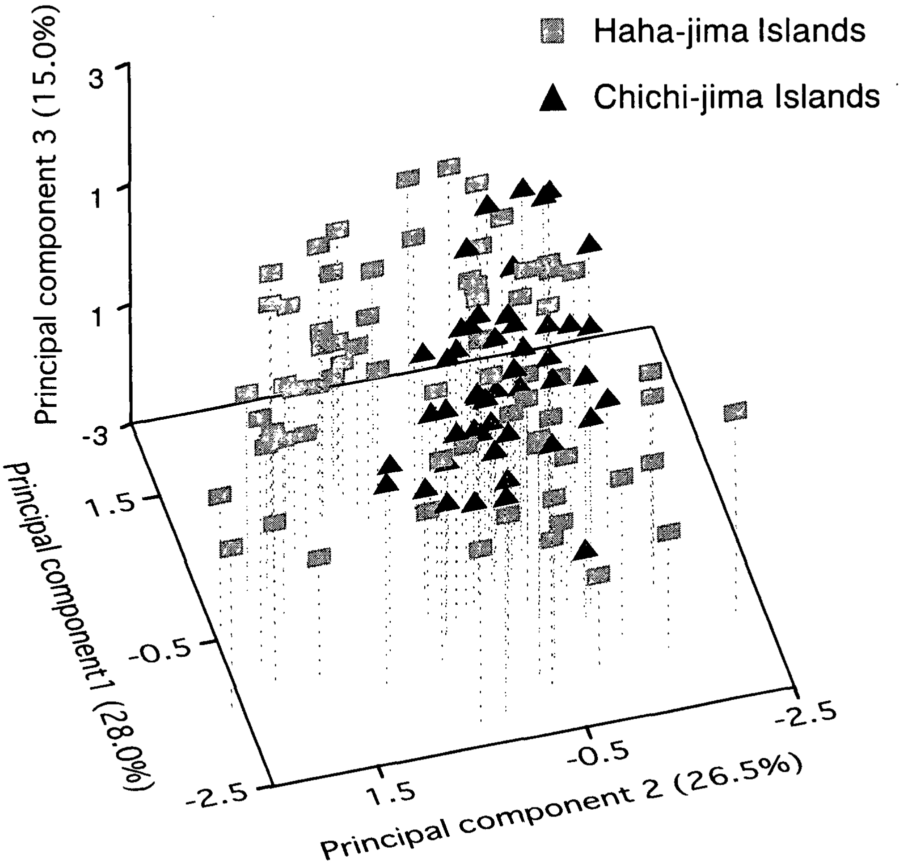

FIG. 4. Three-dimensional diagram of 120 individuals of group A of *Syzygium* in the Chichi-jima Islands and the Haha-jima Islands based on principal component analysis of floral and vegetative characters.

TABLE. 4. Results of principal component analysis for floral and vegetative characters in 133 individuals of group B of *Syzygium* in the Chichi-jima Islands. Code corresponds to that in Fig. 2.

		Component		
Code	Trait	1	2	3
	stem hight	0.00	0.94	0.11
	maximum width of tree crown	0.04	0.91	0.07
A	leaf blade length	-0.94	0.20	0.03
B	leaf blade width	-0.80	-0.44	-0.03
C	length from base of leaf blade to maximum leaf blade width	-0.93	0.24	0.03
D	petiole length	-0.48	0.65	-0.05
E	leaf blade thickness	0.36	-0.49	-0.25
F	pedicel length	0.08	-0.02	-0.12
G	calyx tube length	-0.16	-0.10	-0.81
H	calyx tube width	0.03	-0.15	-0.83
I	style length	0.08	-0.09	-0.77
J	maximum length of filament	0.10	0.05	-0.79
Eigenvalue		2.80	2.70	2.67
Cumulative variance (%)		23.37	45.90	68.12

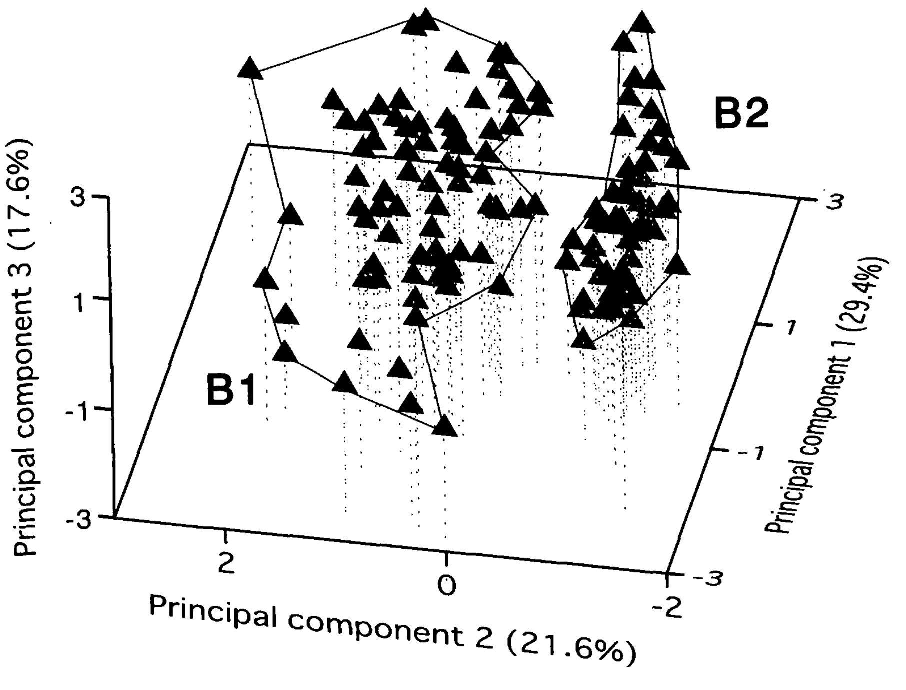

FIG. 5. Three-dimensional diagram of 133 individuals of group B of *Syzygium* in the Chichi-jima Islands based on principal component analysis of floral and vegetative characters.

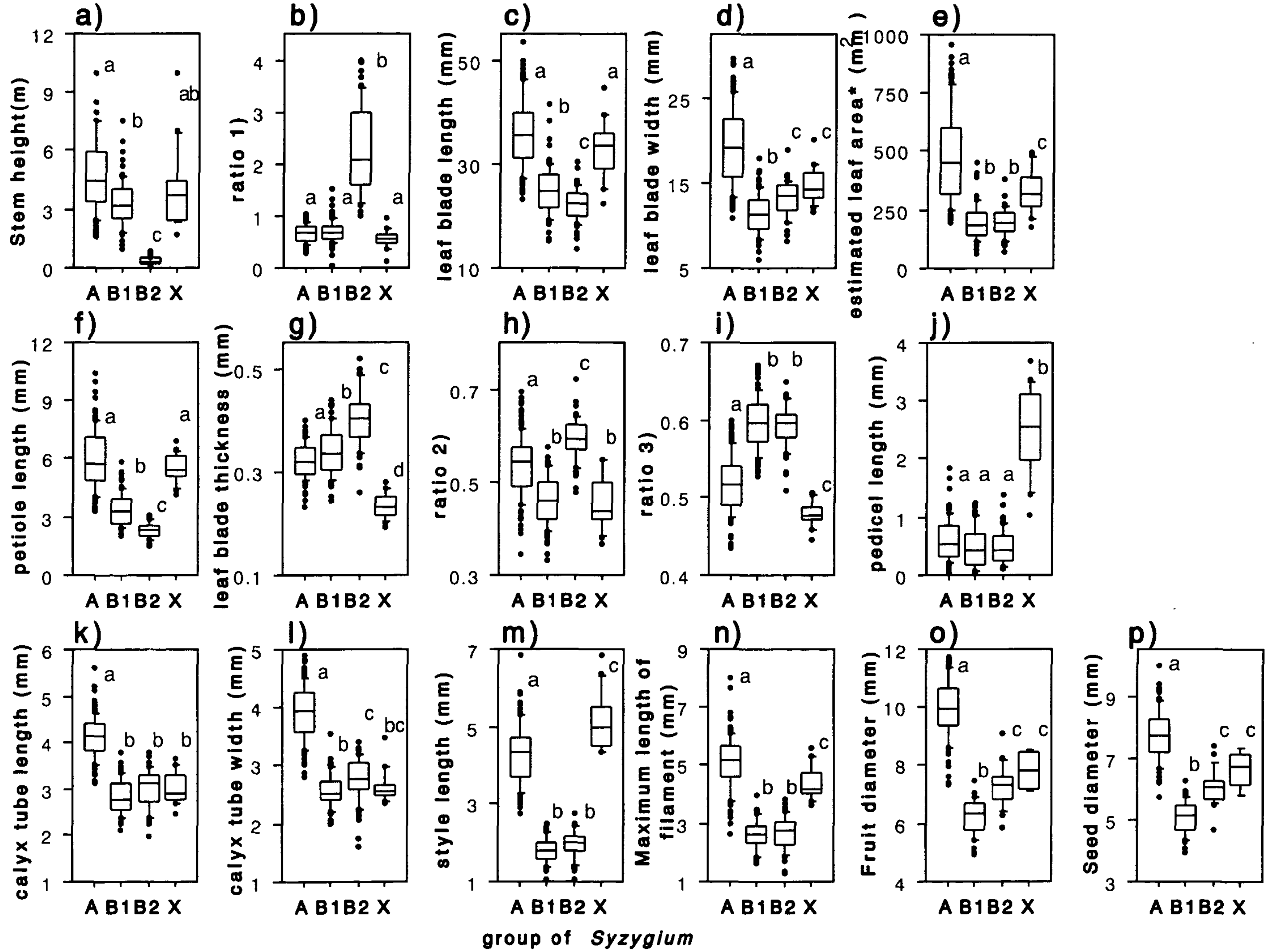

FIG. 6. Morphological variations in four groups of *Syzygium* in the Bonin Islands and the Nansei Islands. A *box* encompasses 25th - 75th percentile interval of data, a *midline* the median. A *vertical bar* represents the 10th - 90th percentile interval, a *dot* a sample out of the interval. The mean or median with the same *letter* show no significant difference among the groups at $p<0.05$ (Steel-Dwass's multiple range test (b), e), h), and i)); Nagata & Yoshida 1997) and Tukey-Kramer's multiple range test (the others).
ratio 1) in b) : maximum width of tree crown / stem height
ratio 2) in h) : leaf blade width / leaf blade length
ratio 3) in i) : length from base of leaf blade to maximum leaf blade width / leaf blade length.
estimated leaf area* in e) : 2 / 3 × leaf blade length × leaf blade width (Whitmore 1990)

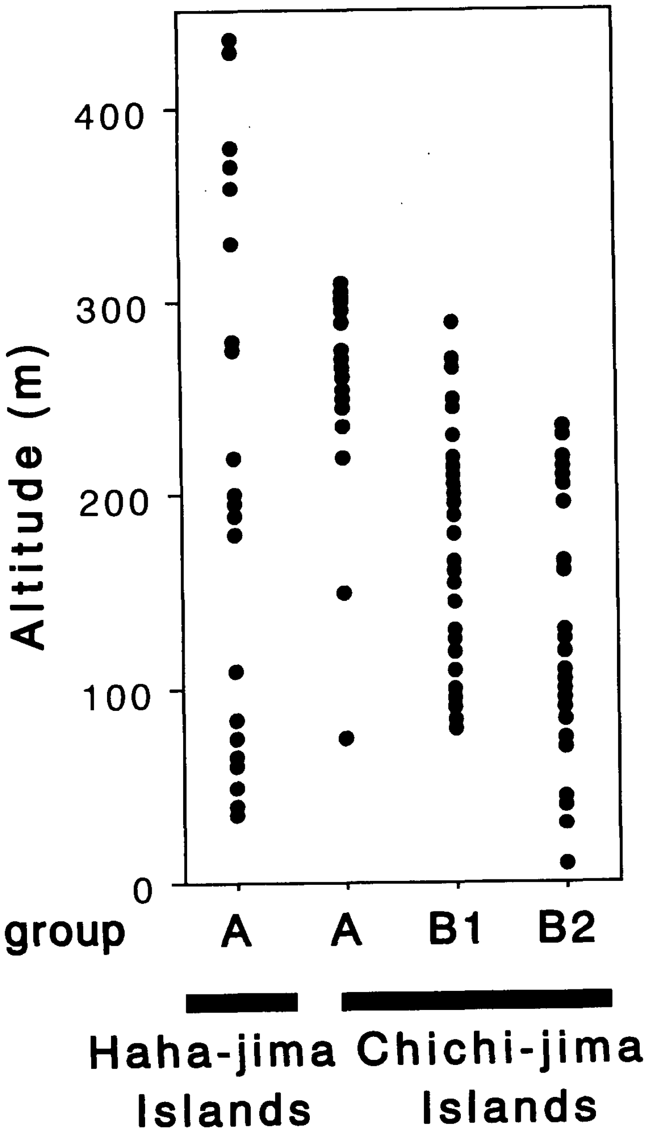

FIG. 7. Altitudinal distributions of the individuals among three groups of *Syzygium* in the Chichi-jima Islands and the Haha-jima Islands.

munities where group A grew, the four communities (community nos. 2, 3, 6, and 11) that distributed only in either the Chichi-jima Islands or the Haha-jima Islands did not assemble as one cluster in the dendrogram. These facts indicate that the floristic composition in plant communities of group A is not so different between the two islands. However in community no. 11 of *Distlylium* - *Schima* dry forest, group A was found only in the Haha-jima Islands but not in the Chichi-jima Islands (Fig. 9). This forest is the main habitat of group B1 in the Chichi-jima Islands. Therefore, this indicates that group A in the Haha-jima Islands also possesses a somewhat different habitat from that of group A in the Chichi-jima Islands.

Group A in the Haha-jima Islands showed remarkable morphological variation among populations in comparison with groups A, B1 and B2 in the Chichi-jima Islands (Fig. 8). Many individuals of group A in the Haha-jima Islands, which occur in community no. 11 of *Distlylium* - *Schima* dry forest, do not overlap with those in the Chichi-jima Islands in the first two principal components (Fig. 10a). These individuals were found mostly at three study sites (study sites 21, 22, and 23 in Fig. 1; Fig. 10c) at 35-110m above sea level, a region which is restricted to the southern peninsula of the Haha-jima Island and the Mukoh-jima Island (Fig. 1 and Table 1). However, the variations of a few individuals at study sites 21 - 23 of the Haha-jima Islands also overlap with those of group A in the Chichi-jima Islands in the first two principal components (Fig. 10a - c). Many characters (Fig. 8b - g, i - n) of the individuals in these study sites are significantly different statistically from those of the other individuals in the Haha-jima Islands at $p<0.01$ (Mann-Whitney U test). The variations in many of these characters have a tendency to shift toward those of groups B1 and B2 in the Chichi-jima Islands (Fig. 8c, g, i - l, and n).

The pre-dawn leaf water potential of group B2 was lower than that of groups A and B1 in the dry summer of 1999 (Fig. 11), which indicates that group B2 actually sustains more intense water stress than groups A and B1 in the summer.

Discussion

Relationship among the four groups of Syzygium *in the Bonin and Nansei Islands, and previous taxonomic treatments*

Three distinct groups are detectable in *Syzygium* of the Bonin Islands by principal component analyses; these three are also distinct from the Nansei Islands group. All the four groups recognized are not characterized

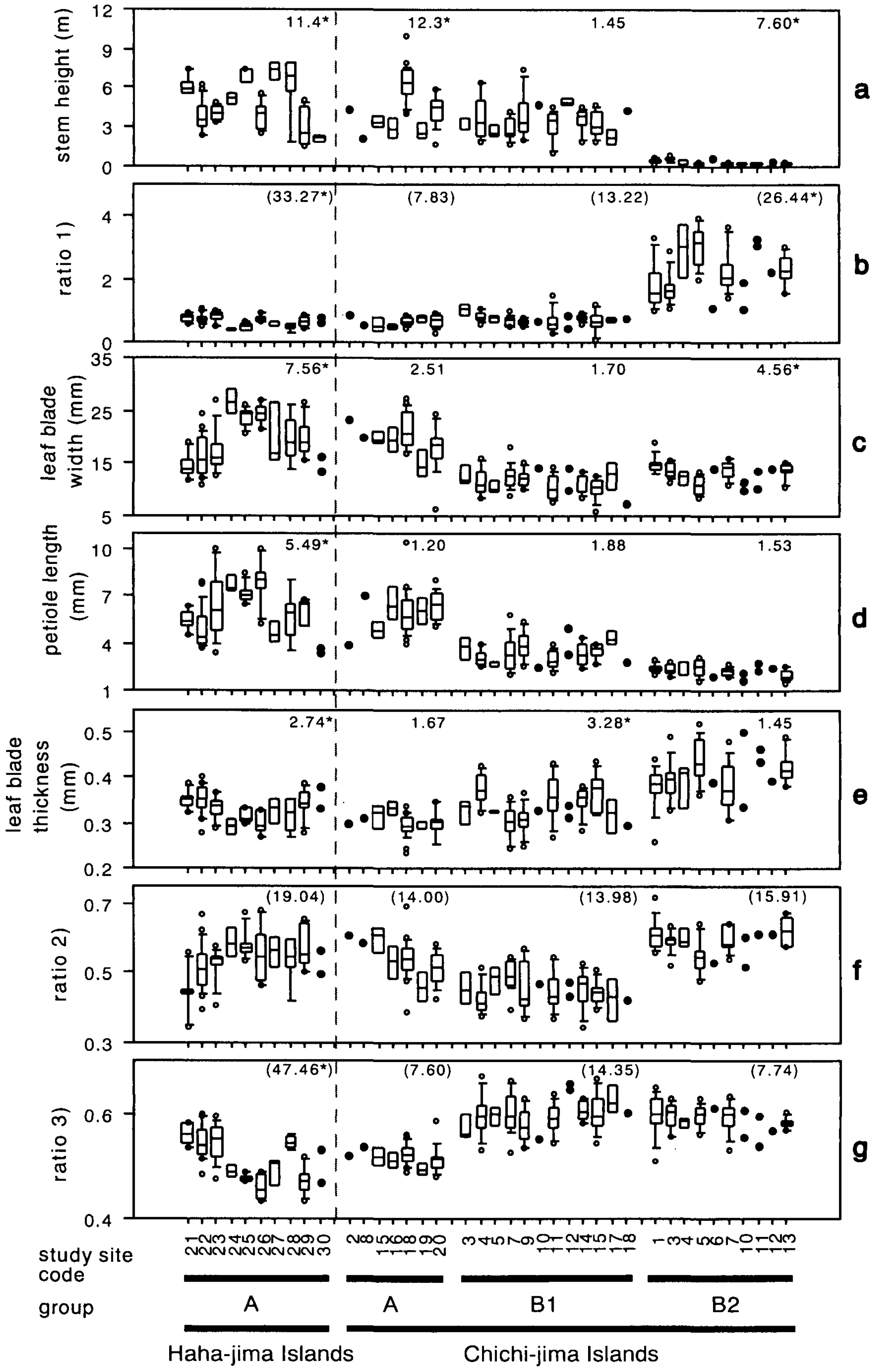

FIG. 8. Populational variations of vegetative and floral characteristics in the three groups of *Syzygium* in the Bonin Islands. *Study site code* corresponds to that in Table 1. A *box* encompasses the 25th - 75th percentile interval of data, a *midline* the median. A *vertical bar* represents the 10th - 90th percentile interval, an *open circle* a sample out of the interval. *Numerals* in each chart represent F value or H, statistic for Kruskal-Wallis test (only b, f, and g) and superscript of numeral (*) shows that the character is significantly different among populations of each group ($p<0.01$; ANOVA or Kruskal-Wallis test).

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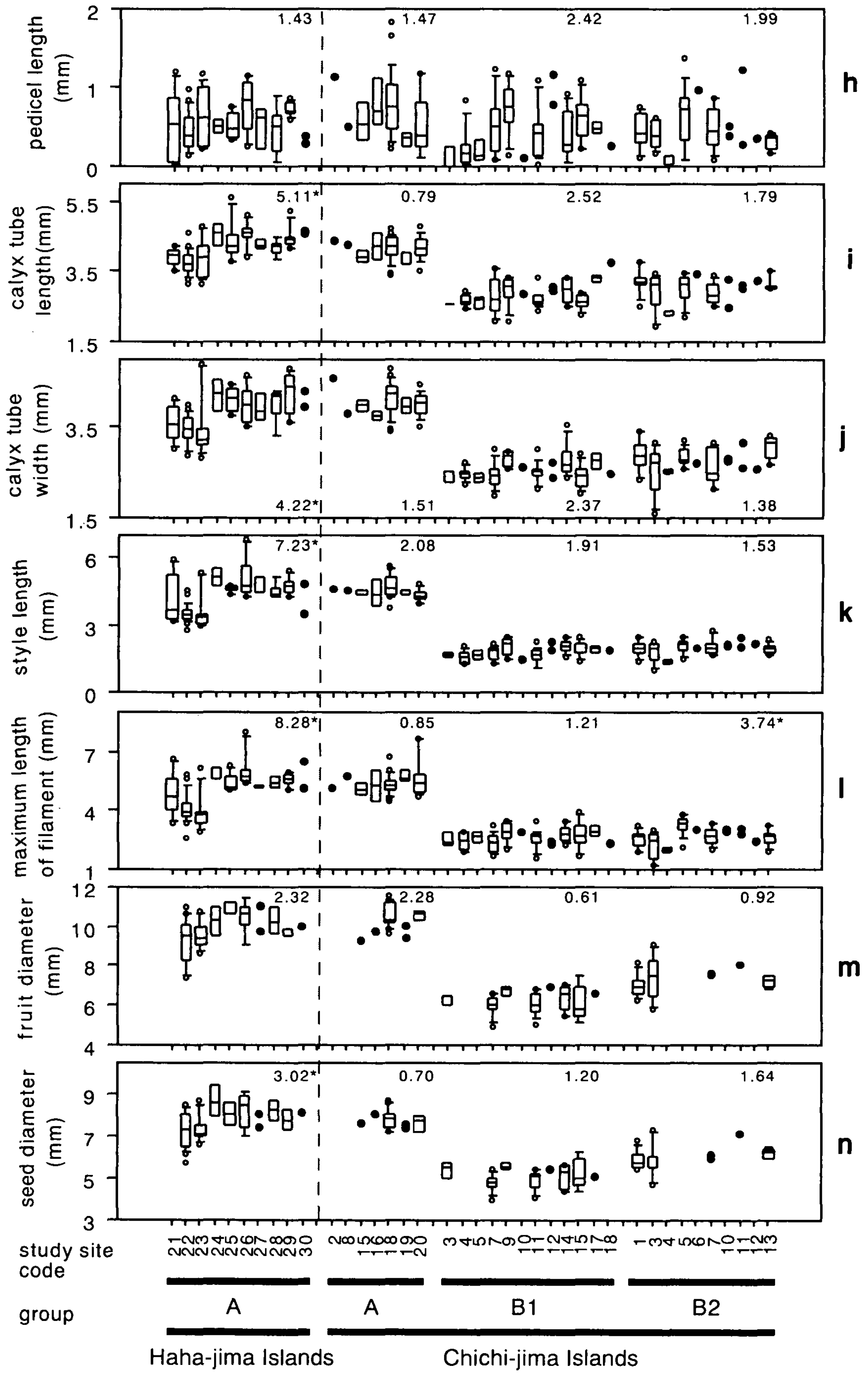

FIG. 8. (continued)

ratio 1) in b : maximum width of tree crown / stem height

ratio 2) in f : leaf blade width / leaf blade length

ratio 3) in g : length from base of leaf blade to maximum leaf blade width / leaf blade length.

by only one major difference, but are distinguished from each other by a combination of morphological characters (Fig. 6). The difference between groups B1 and B2 pertained mainly to vegetative characters (Fig. 6), and the two groups were found to grow in distinct habitats (Fig. 9). One might conclude that these morphological differences simply reflect environmental differences; however, an experimental culture showed that six-month-seedlings of group B1 were different from those of group B2 in leaf thickness, root length / leaf area, and relative growth ratio (RGR) (unpublished data). Hence, it is quite likely that the differences in mature trees from either group are due to genetic, as well as environmental factors. As described, each of the three groups in the Bonin Islands has a peculiar habitat. In some study sites, different groups grow in close proximity, but we could not find intermediates between them on the same islands. Therefore, the four groups seem to be distinct taxonomic groups.

The individuals of the Nansei Islands and of the Bonin Islands are almost distinguishable by the pedicel length, which supports the view of Tateishi (1999). According to Toyoda (1981), some individuals occurring in the Bonin Islands were assigned to *S. buxifolium s. str.*, which is mainly distributed from Japan (Southern Kyushu and the Nansei Islands) to Indochina. However, the present study supports that the populations in the Nansei Islands and those in the Bonin Islands are the different taxa, as proposed by Hatusima (1976, 1989), Tateishi (1999) and Yamazaki (2001).

Tateishi (1999) recognized only one taxon, *S. buxifolium* var. *cleyerifolium*, in the Bonin Islands. Hatusima (1976) recognized two infraspecific taxa in *S. cleyerifolium* (Yatabe) Makino in the Bonin Islands, var. *cleyerifolium* and var. *microphyllum* Hatus.; his distinction was based on leaf shape (obovate or not) and leaf blade length. In our study, however, leaf blade length and leaf shape (length from base of leaf blade to maximum leaf blade width / leaf blade length) varied continuously (Fig. 6c, i). Our four groups are not coincident with the taxonomic views of any of the previous authors. The taxonomy of *Syzygium* in the Bonin Islands will be presented in a forthcoming paper on the basis of our present findings.

Relationship among morphological variation, environmental conditions and distribution of three groups in the Bonin Islands

The pre-dawn leaf water potential of group B2 was lower than that of groups A and B1 in summer (Fig. 11). Davis & Mooney (1986) and Mishio (1992) observed a difference in pre-dawn leaf water potential among co-occurring shrubby species, and attributed it to the evident stratification of their roots. However it is very rare that groups A, B1, and B2 occur sympatrically in one plant community (Fig. 9), and the root stratification of groups A, B1, and B2 is still uncertain. Therefore, it is difficult, at present, to discuss how the degree of their root stratification and soil water content affects the pre-dawn leaf water potential among the groups.

Groups A, B1, and B2 have a tendency to grow in different vegetation in the Chichi-jima Islands (Fig. 9), suggesting that habitudinal segregation occurs among these groups within the Chichi-jima Islands. Similar phenomena are found among endemic congeners of *Pittosporum*, *Symplocos*, and *Callicarpa*, etc. in the Chichi-jima Islands (Shimizu & Tabata 1991). Some of these congeners are reported to have been derived from a common ancestor in the islands (*Pittosporum*: Ito *et al.* 1997, *Symplocos*: Soejima *et al.* 1994).

Plants with small and thick leaves are generally observed in dry habitats (Fahn 1990). It has also been predicted by economic analyses of gas exchange that small leaves are optimal in sunny dry habitats (Givnish & Vermeij 1976). Among the congeners endemic to the Bonin Islands and among infraspecific populations, the species or populations in the severely dry environment of the *Distlylium* - *Pouteria* dry scrub, possess such leaf morphology; in other words, they have thicker and smaller leaves than those habituated in *Distlylium* - *Schima* dry forest (Shimizu 1989). The tendency for thicker leaves in drought-prone habitats is found in *Syzygium* between group B1 in *Distlylium* - *Schima* dry forest and group B2 in *Distlylium* - *Pouteria* dry scrub (Fig. 6g), a fact that is complemented by the finding that group B2 actually sustained heavy water stress than group B1 in summer, 1999 (Fig. 11). However, the leaves of group B2 in *Syzygium* are not significantly smaller than those of group B1 in terms of leaf area (Fig. 6e). Groups B1 and B2 of *Syzygium* may have somewhat different adaptation modes in leaf morphology from the general tendency of adaptation found in other species in the Chichi-jima Islands.

Group A shows remarkable morphological variation of the Haha-jima Islands compared with those of the Chichi-jima Islands. (Fig. 8). Many group A individuals in southern areas of the Haha-jima Islands (study sites 21 - 23 in Fig. 1) have unique morphological sets not found in the other group A individuals on either Haha-jima or Chichi-jima islands (Fig. 10c). The variations in many of these characters have a tendency to shift toward those of groups B1 and B2 (Fig. 8c, g, i - l, and n). As shown in Figs. 9, 10a and 10c, these individuals in study sites 21 - 23 mainly occur in community no. 11, *Distlylium* - *Schima* dry forest. In the *Distlylium* - *Schima* dry forest sites on the Chichi-jima Islands, no group A occurs (Fig. 9). This forest is instead the main habitat of group B1 in the islands. The morphological variation of group A in the Haha-jima Islands is related to its environmental conditions; similar to the pattern in group B1, group A of Haha-jima individuals in *Distlylium* - *Schima* dry forest have smaller leaves, flowers and seeds than group A in *Pinus* - *Schima* mesic forest and *Rhaphiolepis* - *Livistonia* dry forest on the Chichi-jima Islands.

Interestingly, populations of *Callicarpa subpubescens* in the Haha-jima Islands have also been found to be morphologically more variable than those in the Chichi-jima Islands (Kawakubo 1986). The populations of *C. subpubescens* in the Haha-jima Islands with the unique morphological features are located in peculiar habitats (limestone outcrop, and open summits or ridges exposed to wind from the sea; Kawakubo 1986). These populations are not located in *Distlylium* - *Schima* dry forest on the southern, lower-altitude areas of the Haha-jima Islands, but in other forest of higher regions (Mt. Sakai-gatake near study site 30, Mt. Kenzaki-yama near study site 27, etc.). Therefore, the two taxa differed considerably in terms of the geographical and ecological distributions of morphological variation within the Haha-jima Islands.

Pittosporum beecheyi and *Symplocos boninensis*, endemic to the Haha-jima Islands, are probably congeners derived from a common ancestor (Ito *et al.* 1997, Soejima *et al.* 1994), and these species show a tendency to occur in *Distlylium* - *Schima* dry forest (Shimizu 1994). This forest is very narrow and fragmentary in the Haha-jima Islands and is mainly located on southern area of the islands (Shimizu 1994). Hence, Shimizu (1994) has hypothesized that these species might have differentiated from their ancestors in this forest. These species and group A of *Syzygium* grow sympatrically in one vegetation plot of this forest. Indeed, the morphological differentiation within group A of *Syzygium* in the southern area of the Haha-jima Islands may represent an initial stage of the speciation processes, similar to that hypothesized for *Pittosporum* and *Symplocos*.

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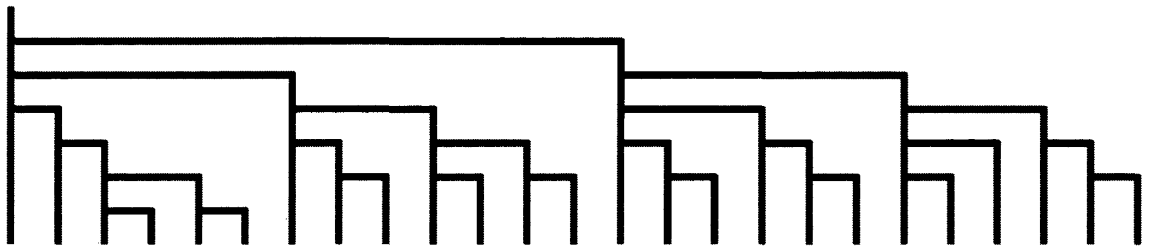

community no.			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
number of plots surveyed			2	3	3	6	4	2	1	5	25	8	22	25	5	3	8	6	3	2	3	3	2	2	4	3	2
mean of vegetation height (m)			2.0	5.1	6.8	6.3	7.1	5.3	0.6	6.6	4.7	2.9	3.9	3.0	4.0	0.6	0.5	0.3	0.5	0.3	0.2	0.7	3.4	1.8	0.8	0.7	0.6
vegetation type (Shimizu & Tabata 1991)			*Pinus* - *Schima* mesic forest						*Rhaphiolepis* - *Livistonia* dry forest			*Distlylium* - *Schima* dry forest				*Distylium* - *Pouteria* dry scrub											
frequency (%) of plots where each group of *Syzygium* occurs																											
occurrence of one group in one plot	Haha-jima Islands	**A**	50	100	0	50	25	0	0	40	8	25	59	8	0	0	0	0	0	0	0	0	0	0	0	0	0
	Chichi-jima Islands	**A**	50	0	100	33	75	100	0	40	44	25	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
		B1	0	0	0	0	0	0	0	0	40	50	36	88	100	0	0	0	0	0	0	0	0	0	0	0	0
		B2	0	0	0	0	0	0	100	0	4	0	5	0	0	100	100	100	100	100	100	100	100	100	100	100	100
sympatric occurrence of two groups in one plot	Chichi-jima Islands	**A** & **B1**	0	0	0	17	0	0	0	20	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

▨ : the communities include the individuals of group A that grow at study site 21, 22, and 23 in the Haha-jima Islands.

☐ : the highest frequency of plots that each group of *Syzygium* occurs on the community

FIG. 9. Dendrogram of plant communities where *Syzygium* plants grow and the distribution of three groups of *Syzygium* in the communities of the Bonin Islands. The communities were clustered by TWINSPAN method (Hill 1979). The vegetation type (Shimizu & Tabata 1991) was determined by floristic composition, vegetation height, and vegetation structure.

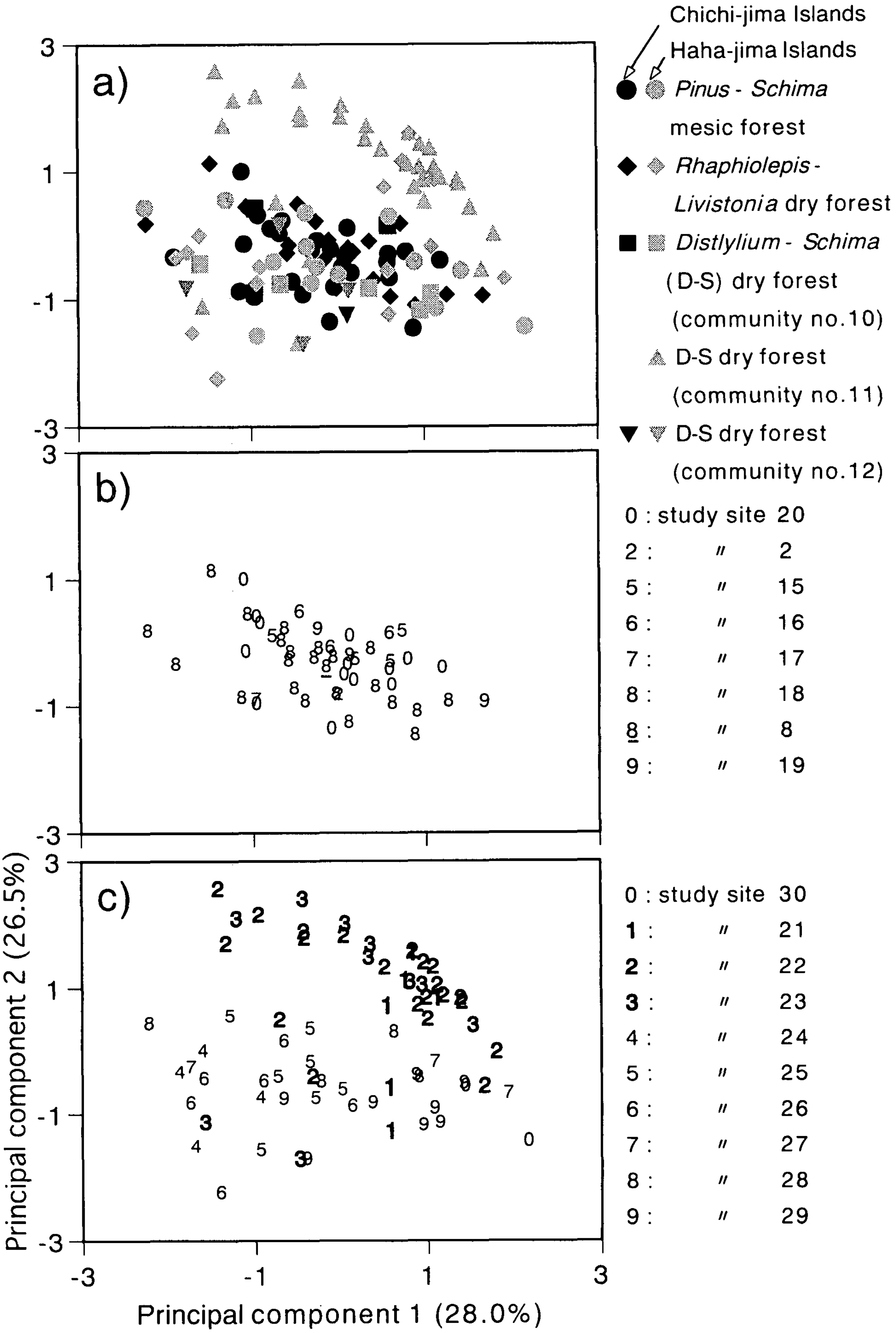

FIG. 10. Scatter diagrams showing relationship between principal components 1 and 2 for all individuals of group A of *Syzygium* a) on each plant community, b) on each study site in the Chichi-jima Islands, and c) on each study site in the Haha-jima Islands.

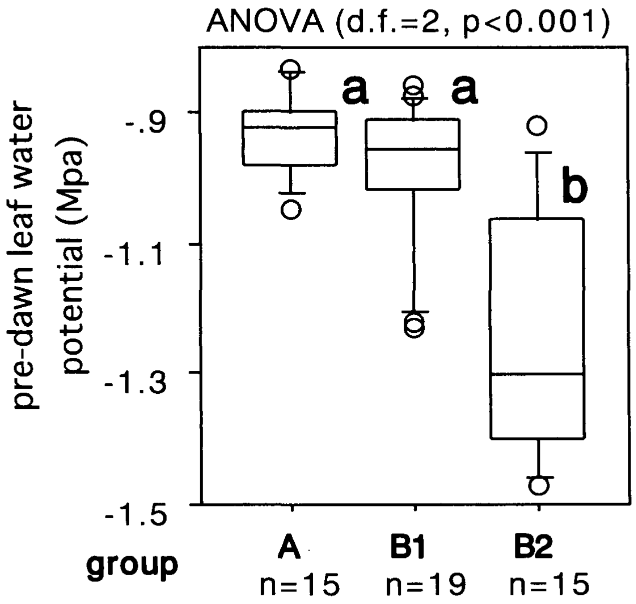

FIG. 11. Pre-dawn leaf water potential of three groups of *Syzygium* in the Chichi-jima Island. The same *letters* in chart indicate that means are not significant different among groups at $p<0.05$ (Tukey-Kramer's multiple range test). "*n*" represents number of individuals.

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